THE SHAPE OF THE SHELL OF THE CHAMBERED NAUTILUS

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(*With a plate*)

Of all the natural beauties, one of the most acclaimed is the shell of the chambered nautilus (*Nautilis* spp.). Painted, drawn, and photographed innumerable times, saluted in poetry, its graceful shape appeals to all viewers, even the artistically ungifted. Scientists too have fallen under its spell and have speculated at length on reasons why the animal builds its shell in one particular shape, a shape that is found also in shells of other molluscs, living and extinct, in ram's horns, in saber teeth, and in other animal structures, as well as in various botanical settings.

After discussing differences in the development of animals and plants displaying a spiral structure, D'Arcy Thompson asserts: "It follows from all this that there cannot be a physical or dynamical, though there may well be a mathematical *law of growth*, which is common to, and which defines, the spiral form in *Nautilus*, in *Globigerina*, in the ram's horn, and in the inflorescence of the sunflower" (1971). From all the properties of the logarithmic spiral, he selects as the key one its continued similarity with itself as it grows.

This is assuredly a beautiful and unique property of the logarithmic spiral, but it asks a lot of the animal that builds the shell. The creature must constantly be surveying the whole of its past shell-work to keep its current addition in line with the global requirement of self-similarity. We prefer to give a local explanation for the shape and we offer one that is biologically simple and plausible and, moreover, does not require the animal to know any mathematics. The basic hypothesis certainly can be experimentally tested in a number of different situations. Our explanation is biologically dynamic and not merely descriptive and numerological, as phyllotaxis is.

We suppose that, as the shell is enlarged, the shape of the rim (or tube cross-section) remains similar to itself. We suppose that the animal deposits new shell material at the rim at a rate proportional to the circumference of the rim. (There is, furthermore, some mechanism to keep the shell attached to itself as it coils.) Finally there is a condition, to be explained later, for which we can think of no name better than "embryological predisposition".

Using polar coordinates, express the equation of the shell coils as $r = f(\theta)$. Because of the similarity of cross-sections, the circumference of the rim is proportional to a characteristic length, say the "height" of the tube: $f(\theta) - f(\theta - 2\pi)$. Since the rate of deposit of shell material is then proportional to that height, there is a constant k so that

$$f'(\theta) - f'(\theta - 2\pi) = k[f(\theta) - f(\theta - 2\pi)].$$

It is easy to verify that $f(\theta) = f(o) \exp k\theta$ is a solution of this differential-difference equation.

It is crucial to note that, under a suitable condition, the solution just found is unique. To see this, suppose f to be a specified differentiable function when $-2\pi \leq \theta \leq o$. Then the equation can be thrown into the form

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$$f'(\theta)-kf(\theta)=f'(\theta-2\pi)-kf(\theta-2\tau).$$

This can be treated as a linear differential equation with known forcing function on the interval $o \leq \theta \leq 2\pi$ and the solution, which is unique, can be written out explicitly if desired. The process can be repeated on the next interval $2\pi \leq \theta \leq 4\pi$, and so on. Hence, it is enough to specify f for $-2\pi \leq \theta \leq o$ and this the animal does in some still unknown way. This is what we referred to as the "embryological predisposition". (It is, of course, a mystery of science but, we think, a genuine and biologically relevant mystery in contrast to numerological ones such as phyllotaxis.)

The foregoing applies as well to other gastropods. Furthermore, it covers the ammonites, an extinct genus of cephalopods, which do not spiral inward toward a point but instead toward a limit circle.

References

D'Arcy Thompson, (1971): On Growth and Form (Abridged Edition, J. T. Bonner, ed.), Cambridge University Press, pp. 173-174. This edition has references to recent work on phyllotaxis. For a survey of older work on phyllotaxis, see the earlier editions of Thompson's book.